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The Relationship Between Language Ability and Brain Activity Across Language Processes and Modalities

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Abstract

Existing neuroimaging studies on the relationship between language ability and brain activity have found contradictory evidence: On the one hand, *increased* activity with higher language ability has been interpreted as deeper or more adaptive language processing. On the other hand, *decreased* activity with higher language ability has been interpreted as more efficient language processing. In contrast to previous studies, the current study investigated the relationship between language ability and neural activity across different language processes and modalities while keeping non-linguistic cognitive task demands to a minimum. fMRI data were collected from 22 healthy adults performing a sentence listening task, a sentence reading task and a phonological production task. Outside the MRI scanner, language ability was assessed with the verbal scale of the Wechsler Abbreviated Scale of Intelligence (WASI-II) and a verbal fluency task. As expected, sentence comprehension activated the left anterior temporal lobe while phonological processing activated the left inferior frontal gyrus. Higher language ability was associated with increased activity in the left temporal lobe during auditory sentence processing and with increased activity in the left frontal lobe during phonological processing, reflected in both, higher intensity and greater extent of activations. Evidence for decreased activity with higher language ability was less consistent and restricted to verbal fluency. Together, the results predominantly support the hypothesis of deeper language processing in individuals with higher language ability. The consistency of results across language processes, modalities, and brain regions suggests a general positive link between language abilities and brain activity within the core language network. However, a negative relationship seems to exist for non-linguistic cognitive functions located outside the language network.

Keywords: fMRI, sentence comprehension, phonological processing, verbal intelligence, neural efficiency

1. Introduction

The neuroimaging literature offers a large number of studies that investigage the neural correlates of language processing for the purpose of localizing its different components in the brain. These studies have reached some consensus about the brain areas involved in language processes such as phonology, semantics, and syntax (Hickok & Poeppel, 2007; Price, 2010; Vigneau et al., 2006). In contrast, the number of neuroimaging studies focusing on the role of individual differences, such as participants' language ability, in the neural correlates of language processing, is comparatively small.

Language ability is a multidimensional concept that covers a wide range of linguistic processes. It has previously been operationalized as, for example, verbal working memory span, vocabulary size, or high-level language abilities such as metaphor processing and inference generation (Prat & Just, 2011; Van Ettinger-Veenstra, Ragnehed, McAllister, Lundberg, & Engström, 2012). Individual differences in language ability have been linked to differences in brain activity during language processing but the exact nature of the relationship is still unclear. In fact, higher language ability has been associated with both, increases and decreases in neural activity, and there has been considerable variation regarding the brain areas in which activity shows an effect of language ability. Furthermore, a range of interpretations has been offered to explain the various findings.

1.1 Positive relationships between language ability and brain activity

Positive relationships between language ability and brain activity are characterized by increased brain activity during language processing in individuals with higher language ability compared to individuals with lower language ability. This increased activity has typically been interpreted in the light of superior language processing in higher-ability individuals. For example, increased activity in areas of the cortical language network, such as the left angular gyrus, Broca's area, and the left temporal lobe, has been hypothesized to reflect deeper semantic processing and greater sensitivity to semantic relationships between sentences during comprehension tasks (Prat et al., 2011; Van Ettinger-Veenstra et al., 2016). A similar

effect can be found when comparing brain activity during comprehension of texts on familiar versus unfamiliar topics, which could also be explained with deeper semantic processing of familiar than unfamiliar contents (Buchweitz, Mason, Meschyan, Keller, & Just, 2014; St George, Kutas, Martinez, & Sereno, 1999).

Other studies have found activity increases with higher language ability in brain areas that are not part of the core language network, such as right-hemisphere homologues of typical language areas (Van Ettinger-Veenstra et al., 2012), or brain areas associated with executive and memory functions (Prat & Just, 2011). Activity increases in these two sets of brain areas have been interpreted as a positive modulation of task demands (Van Ettinger-Veenstra et al., 2012) or a "neural adaptability" in high-ability individuals, describing a dynamic recruitment of additional brain areas based on the requirements of the task at hand (Prat, 2011; Prat & Just, 2011). Right-hemispheric and frontal executive areas are also more activated when processing unfamiliar compared to familiar texts (Buchweitz et al., 2014; St George et al., 1999). These findings were interpreted in the light of working-memory and strategic processes which can aid comprehension when the reader/listener does not have the necessary background information to easily understand the text.

1.2 Negative relationships between language ability and brain activity

Negative relationships between brain activity and language ability have typically been interpreted as neural efficiency. Neural efficiency is characterized by reduced brain activity in individuals with higher ability than those with lower ability, in combination with equal or even superior performance (Prat, 2011; Prat, Keller, & Just, 2007). The relative reduction in activity is thought to reflect the reduced effort that individuals with higher ability need to invest when performing a task, consequently saving neural resources compared to individuals with lower levels of ability. Interpretations of neural efficiency during language processing have been proposed for negative correlations in left-hemisphere language areas such as the IFG (Prat & Just, 2011), right-hemisphere homologues (Prat, Mason, & Just, 2012), and areas associated with executive and memory functions (Prat & Just, 2011; Prat et al., 2007). Other researchers

have suggested automatization processes to explain reduced neural activity in subjects with high language ability, with skilled readers engaging in more automated and hence more efficient processing (Welcome & Joanisse, 2012).

For negative correlations between language ability and brain activity located in the right hemisphere specifically, yet another explanation has been proposed. The dynamic spillover hypothesis (Prat, Mason, & Just, 2011; Prat, Mason, & Just, 2012) proposes that the right hemisphere is capable of processing language, though not as efficiently and precisely as the left hemisphere. Therefore, the right hemisphere is only used as a reserve when task demands are high and part of the processing "spills over" into the right-hemisphere homologues of the already occupied typical left-hemisphere areas. Since individuals with lower language ability experience higher demands when processing language than higher-ability individuals, their left-hemisphere capacities are thought to be exhausted more quickly. Consequently, individuals with lower language ability resort to right-hemisphere areas to a greater degree, resulting in negative correlations between ability and activity in the right hemisphere (Prat et al., 2011).

In summary, while neural activity during language processing has repeatedly been shown to vary with individuals' language ability, the direction of the relationship and the location of the effects in the brain are unclear. Furthermore, some of the interpretations that have been offered to explain the various findings are in contradiction with each other. For example, neural efficiency and neural adaptability have both been suggested as signs of higher-ability subjects' superiority when processing language, even though they are characterized by opposing findings (i.e., negative relationships and positive relationships, respectively). For example, the engagement of the right hemisphere and brain areas related to executive functions has been suggested as a response to increased task demands. However, this explanation has been employed as an interpretation for positive correlations (Van Ettinger-Veenstra et al., 2012; Prat & Just, 2011) as well as negative correlations (Prat et al., 2011; 2012). In other words, additional recruitment of neural resources is described as adaptive when found in subjects

with higher language ability (Prat & Just, 2011; Van Ettinger-Veenstra et al., 2012) but as a lack of efficiency when found in subjects with lower language ability (Prat et al., 2011; 2012).

1.4 Language-specific effects versus domain-general cognitive demands

So far, the factors that give rise to positive correlations between language ability and brain activity in some instances and negative correlations in other instances are unclear. These factors are particularly difficult to identify because the studies described above typically find a mixture of positive and negative correlations, usually for the same task and - across studies - in the same brain areas (e.g., Buchweitz, Mason, Tomitch, & Just, 2009; Prat et al., 2011; Van Ettinger-Veenstra et al., 2012). Therefore, it seems unlikely that the direction of the relationship is merely an effect of the task, with specific tasks eliciting positive and other tasks eliciting negative correlations. It is, however, possible that different aspects of the tasks that have been used (i.e., different cognitive demands required for task performance) are differentially susceptible for positive versus negative correlations.

Most of the studies investigating the relationship between language ability and brain activity have investigated activity derived from sentence reading paradigms. However, the specific task that participants had to perform while reading, varied between paradigms and involved, for example, answering questions about sentence meaning (e.g., Buchweitz et al., 2009; Van Ettinger-Veenstra et al., 2016), integrating information from working memory (e.g., Prat & Just, 2011; Prat et al., 2012), or completing sentences (e.g., Van Ettinger-Veenstra et al., 2016). It is difficult to determine how these differing task requirements contribute to the activations that have been found in the studies. This is particularly true for activations in the right-hemisphere and executive functioning areas that are not typically involved in language processing per se, with the exception of text-level language processing (Ferstl, Neumann, Bogler, & von Cramon, 2008; Ferstl & von Cramon, 2001). It is possible that, when comparing subjects with relatively higher versus lower language ability, differences in activations do not solely stem from differences in language-specific activations but also from differences in activations associated with general cognitive demands imposed by a particular task. It has

been suggested that domain-specific abilities, such as language ability, and domain-general abilities, such as executive functions, might show differential relationships with brain activity (Neubauer & Fink, 2009). Specifically, higher domain-specific abilities seem to be related to increases in neural activity, whereas higher domain-general abilities seem to be related to decreases of activity, which could explain the mixture of positive and negative correlations that were found between language ability and brain activity in the studies mentioned above. Finally, language paradigms that are high in cognitive demand might also result in behavioral differences between higher-ability and lower-ability individuals. Differences in activations might then reflect differences in processing, such as cognitive engagement or performance levels, rather than differences in ability per se (Prat, 2011).

On the contrary, language paradigms that are low in domain-general cognitive demand might offer an alternative way to give insight into the relationship between language ability and language-specific neural activity. For example, Virtue, Parrish, and Jung-Beeman (2008) used a passive story listening paradigm to study the neural correlates of inference generation. While participants were asked to answer comprehension questions at the end of the fMRI runs, there was no additional task interfering with basic language processing while listening to the stories. On the group level, inference generation activated the bilateral inferior frontal gyri and bilateral temporal gyri as would be expected (Ferstl, Neumann, Bogler, & von Cramon, 2008; Jung-Beeman, 2005). Neural responses in the right temporal gyrus (overlapping with whole-group activation) were positively correlated with performance on a reading span task, suggesting enhanced processing and inference generation in individuals with higher language ability. Thus, these results suggest a positive relationship between language ability and activity for paradigms that are low in domain-general cognitive demand and rely on stimulus-driven “pure” language processing.

The study reported here used fMRI to investigate the neural correlates of language processing while keeping domain-general task demands at a minimum. Brain activation during sentence processing (in listening and reading) and phonological processing (in repetition) were

correlated with two measures of language ability. First, the Verbal Comprehension Index (VCI, formerly known as verbal IQ) was assessed with the verbal subscale of the Wechsler Abbreviated Scale of Intelligence (WASI-II). The VCI is a well-established measure of language ability that has been validated in a large sample of subjects spanning different age groups (Wechsler, 2011). Second, the verbal fluency (VF) task was chosen a well-established paradigm that has frequently been used to assess individuals' semantic and phonological fluency (e.g., Birn et al., 2010; Costafreda, Fu, Lee, Everitt, Brammer, & David, 2006). While these two language ability measures assess, to some extent, similar abilities (e.g. vocabulary size), they also differ in important ways. Specifically, the VF test is not only strongly associated with linguistic ability but also reflects aspects of executive functioning (Aita, Beach, Taylor, Borgogna, Harrell, & Hill, 2018). Including both, the VCI and VF in the current study will allow for a more comprehensive assessment of the relationships between ability and brain activity. The shared linguistic requirements of the two measures should lead to some overlap in findings and could give an indication about the reliability and generalizability of the results across different language ability measures. On the other hand, the assessment of aspects of executive functioning, which constitute a part of VF but less so of the VCI, can shed light on the role of non-linguistic, domain-general cognitive abilities for brain activity during language processing.

Given the language-specific processing demands of the fMRI paradigm, effects of language ability on brain activity were expected to be located primarily in language-related brain areas. Specifically, we expected activity in left-hemisphere temporal regions during sentence processing and activity in left frontal regions during phonological processing to vary with the VCI and VF. Despite the contradictory findings regarding the direction of potential relationships in previous studies, correlations were predicted to be primarily positive in the current study, based on similarities of this study's low-effort, language-focused task paradigm with previous stimulus-driven, passive paradigms (Virtue et al., 2008) and existing hypotheses about positive ability-activity relationships for domain-specific abilities (Neubauer & Fink,

2009). VF was expected to show additional negative relationships with brain activity in areas outside the traditional core language network, due to its executive functioning components.

2. Methods

2.1 Subjects

Twenty-six right-handed native English speakers were recruited through the Durham University participant pool and gave informed consent to take part in the study. They had normal or corrected-to-normal vision and normal self-reported hearing. All participants reported no history of psychiatric or neurological conditions. After motion correction, four participants were excluded due to movements greater than one voxel size between volumes, leaving a sample of twenty-two subjects (14 female, mean age 22.05 years, *SD* = 7.66, range 18-55). The Edinburgh Handedness Inventory (Oldfield, 1971) revealed a mean handedness index of 83.13 (*SD* = 20.18, range 41.18 - 100). The study was approved by the Durham University Ethics Committee and conformed to the guidelines of the Declaration of Helsinki.

2.2 Stimuli

Different types of language stimuli as well as modality-specific control stimuli were used to tap into different language processes. The language stimuli included sentences, words and pseudowords. All words were taken from the MRC Psycholinguistic Database (Coltheart, 1981). Pseudowords were generated based on those words, using the Wuggy software (Keuleers, & Brysbaert, 2010). FMRI data for processing of pseudosentences and scrambled sentences were also collected as part of a different project and are not reported in the current paper.

The word condition consisted of lists of nouns only, in order to avoid the possibility of grammatically combining words into sentences. For all nouns, used in the word and sentence conditions, the mean number of letters was 6.11 (*SD* = 2.00), mean word frequency per million was 74.13 (*SD* = 118.04), the mean familiarity was 528.82 (*SD* = 76.71), and the mean

concreteness was 514.31 (*SD* = 101.40). Across subjects, the same stimuli were used in the three modalities, listening, reading, and repetition.

The sentences consisted of six to seven words and all sentences had the same grammatical structure (i.e., active sentences with subject – verb – object, including adjective). The majority of sentences had several possible ending words. One of those words was presented as the last word in a sentence. The other ones were presented in the word condition (see Table 1 for examples). This way, the same nouns were used in the word lists and in the sentences across participants. Across conditions, a total of 1009 content words was used, 533 of which were nouns, 238 of which were verbs, and 238 of which were adjectives.

Auditory control stimuli were created in the Audacity software by temporally reversing the pseudowords used in the pseudoword condition. Visual control stimuli were generated from words in the word condition by replacing half of the letters of the alphabet with / and the other half with \. This resulted in length-matched stimuli in the form of, for example "/ / \ /" or "\ / / / \ /".

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Insert Table 1 about here

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2.3 Procedure

2.3.1 Behavioral testing

In addition to the fMRI sessions, all participants performed further language tasks outside the scanner, typically on the day before their scanning session.

Verbal Comprehension Index (VCI). The verbal subscale of the Wechsler Abbreviated Scale of Intelligence (WASI-II) was administered, consisting of the Vocabulary test and the Similarity test (Wechsler, 2011). Participants' answers were scored according to the WASI-II manual and converted into the Verbal Comprehension Index using the normative data provided by the WASI-II.

Verbal Fluency (VF). Participants performed a verbal fluency task, consisting of a semantic part (e.g., Basho et al., 2007; Birn et al., 2010; De Carli et al., 2007) and a phonological part (known as the Controlled Word Association Test (COWAT), e.g. Loonstra et al., 2001; Rodriguez-Aranda & Martinussen, 2006). In the semantic part, participants were given two minutes to name as many words as they could, belonging to a certain category (i.e., animals, fruits, jobs). In the phonological part, participants were given two minutes to name as many words as they could, starting with a certain letter (i.e., F, A, S). The number of words generated per category and letter was used as a measure of semantic and phonological fluency, respectively.

2.3.2 fMRI paradigm

The fMRI data were acquired during a passive listening task, a silent reading task and a repetition task. Before scanning, participants were instructed to listen/read attentively and to press a button after each stimulus, as soon as the word/sentence was finished. This task ensured that participants stayed alert and processed the stimuli appropriately while keeping language-unrelated cognitive demands minimal and constant across the different modalities and stimulus types. In the repetition blocks, the button press was followed by the participant repeating the stimulus out loud. Participants switched hands for responding during a break halfway through the experiment, counterbalancing the order of left and right hand across participants.

Data were acquired over two sessions with three identical runs each (listening 19.2 min, reading 15.0 min, repetition 13.1 min), only changing the specific stimuli that were presented. The order of runs (i.e. modalities) was counterbalanced and the order of conditions in each run was determined by one of four pseudorandomly generated lists of conditions. Each condition had eight blocks per modality in total. In addition, there were eight blocks of a low-level baseline condition (looking at a fixation cross, 37.5 sec). Each block was preceded by a prompt screen which was presented for 2 sec, indicating the condition. Between the two scanning sessions, participants had a break of approximately one to two hours. Each session

lasted about one hour, including short breaks between the three runs and a structural scan (T1 or DTI) at the end of the session.

All stimuli were presented with the Psychtoolbox-3 software, run under MATLAB version R2014a. Auditory stimuli were presented through fMRI compatible in-ear headphones at a comfortable, audible listening volume verified by the participant. During the auditory stimulus presentation, participants were instructed to fixate a white cross presented at the center of a screen in front of them. Visual stimuli were presented on an MR-compatible screen (Cambridge Research Systems) placed at the back of the scanner which participants viewed via a mirror attached to the head coil. Participants viewed the screen by a mirror mounted on the head coil. Stimuli were presented in white font in the center of a black screen. Stimulus presentation in the repetition runs was identical to the listening runs, except for longer ISI to allow for repetition of the stimuli by the participant. Interstimulus intervals (ISI) were jittered in all conditions. In total, 112 words/pseudowords and 48 sentences/pseudosentences were presented per modality (except for repetition, where it was 56 and 24 respectively). Details on the number and durations of stimuli and ISI per condition and modality are given in supplementary tables S1-S3.

2.4 fMRI data acquisition

Data were acquired on a Siemens 3T Magnetom Trio Scanner in the James Cook University Hospital, Middlesbrough, UK, using a 32-channel head coil. EPI imaging of the whole head was performed, using a 96 x 96 matrix with a field of view of 210 and a voxel size of 2.1875 x 2.1875 x 3 mm. 35 axial slices were collected in ascending acquisition with a 10% gap between slices. The TR was 2.16 s, TE 30 ms and the flip angle was 90°. The total number of volumes acquired per person (across the two sessions) was 2660: 1080 for listening runs, 844 for reading runs, and 736 for repetition runs.

Anatomical data were acquired with a T1-weighted 3D sequence comprising 192 slices (TR = 2250 ms, TE = 2.52 ms, TI = 900 ms; flip angle 9°, FOV = 25.6cm, 512x512 matrix, voxel size = 0.5x0.5 mm).

2.5 Data preprocessing and analysis

Data were preprocessed and analyzed using FSL (FMRIB's Software Library, version 4.1, http://www.fmrib.ox.ac.uk/fsl) using a standard preprocessing pipeline. For each subject, two first-level analyses were performed, one for each of the two fMRI sessions. Motion correction was carried out using FSL's MCFLIRT and motion parameters (and their first derivatives) were later included in the model as regressors of no interest. The mean volume-to-volume motion in the sample, calculated as the Euclidean distance $\text{sqrt}(x^2+y^2+z^2)$ was 0.08 voxels (the mean of excluded subjects was 0.17). Data were high-pass filtered with the cut-off set to twice the maximum cycle length for each of the runs (Poldrack et al., 2012), resulting in 168 s for listening runs, 140 s for reading runs and 152 s for repetition runs. Images underwent default FSL linear normalization to MNI (Montreal Neurological Institute) standard space with 12 degrees of freedom and were spatially smoothed with a full-width half-maximum kernel of 6 mm. In an event-related analysis, each stimulus type was modelled as an explanatory variable and convolved with a double gamma hemodynamic response function. Resting blocks were used as an implicit baseline not specified in the model.

Three contrasts were chosen to reflect the different language processes that were investigated: listening to sentences > auditory control for auditory sentence comprehension; reading sentences > visual control for visual sentence comprehension; repeating pseudowords > repeating words for phonological processing. Due to their regular use, words have a stored sensory and motor representation and their production is therefore phonologically less demanding than the production of pseudowords (Hickok, 2009; Hickok & Poeppel, 2007; Saur et al., 2008).

For each participant, first-level results were combined in a second-level fixed effects analysis. The results of the second-level analysis were fed into a between-subjects analysis using FSL's FLAME 1+2. Outliers were automatically de-weighted by the software. All results were corrected for multiple comparisons using the FSL default cluster-thresholding procedure ($z > 2.3$, $p < .05$).

In the group-level analysis, the behavioral data collected outside the scanner were included as covariates. VCI scores and VF scores were entered as explanatory variables and orthogonalized with regard to the main effect of stimulus type (i.e., demeaned). Hence, results reflect brain areas where activity varies with performance on the VCI and the VF task, respectively. Positive contrasts (e.g., sentences > control) show positive correlations between language ability and the BOLD signal change (i.e., more positive signal change for participants with higher language ability), whereas the reverse contrasts show negative correlations. For each language process, covariate effects were masked with unthresholded contrast images from the respective language process versus the resting baseline (e.g., covariate effects for sentences > control were masked with sentences > resting baseline). This was done in order to only show effects that were associated with the process of interest (e.g., sentence processing) rather than effects associated with the control condition. Correlations were quantified by performing Pearson correlation analyses on the ability scores and beta weights extracted with FSL FEATquery.

3. Results

3.1 Behavioral results

Verbal Comprehension Index. The mean WASI-II VCI, comprised of participants' scores on the Vocabulary test and the Similarity test, was M = 120.14 (SD = 14.80).

Verbal Fluency. In the semantic VF task, participants generated a mean of 27.08 words within two minutes (SD = 4.74). Performance in the phonological VF task was slightly lower with 22.15 words (SD = 6.27). The mean overall VF was M = 24.61 (SD = 5.04). Performances on the two subparts were significantly correlated, $r(20) = .67$, $p = .001$, two-tailed. VF showed a significant positive correlation with the VCI, $r(20) = .460$, $p = .031$, two-tailed.

3.2 fMRI group activations

Group activations for auditory sentence comprehension were predominantly located in the left temporal lobe, with the strongest activation in the temporal pole. In the reading modality,

sentence comprehension resulted in similar but more widespread activation in the left temporal lobe. Additionally, activation was found in right temporal areas and left frontal regions. Phonological processing during pseudoword repetition resulted in pronounced activations in the left inferior frontal gyrus, middle frontal gyrus, precentral gyrus and insula. Further activations were found in the paracingulate and medial superior frontal gyrus and right frontal areas. All group activations are displayed in Figure 1 and information on activation peaks and brain areas covered can be found in supplementary tables S4-S7.

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Insert Figure 1 about here

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3.3 Behavioral covariates

Covariate analyses revealed significant relationships between brain activity and language ability. For auditory sentence comprehension, activity in the left temporal gyrus showed positive correlations with the VCI and VF, with covariate effects in the left temporal pole, anterior and posterior STG, MTG, and ITG. There was considerable overlap between areas of correlation for the VCI and VF, and both ability measures partly overlapped with the mean group activation for auditory sentence comprehension (Figure 2). In addition, negative correlations were found between VF and auditory sentence comprehension activity in right auditory areas (see appendix S8 for a table with all peaks).

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Insert Figure 2 about here

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Activity for sentence comprehension in reading showed no significant correlation with the VCI but did vary with VF. There were no positive correlations but a negative correlation between VF and activity in right occipital regions and right precentral gyrus (see Appendix table S9).

For phonological processing, activity in the left inferior frontal gyrus (pars opercularis) and precentral gyrus was positively correlated with the VCI and VF, extending into the postcentral gyrus for the latter (Figure 3, table A6). No negative correlations were found between the activity during phonological processing and the VCI or VF.

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Insert Figure 3 about here

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The partial overlap of covariate effects and group activations as described above suggests that some brain areas are activated in participants with higher language ability as well as participants with lower language ability, only more strongly so in higher-ability participants. In contrast, brain areas that show a covariate effect but no group activation might only be activated in participants with higher language ability. To explore these differential patterns, BOLD responses were investigated separately in brain areas with overlapping group activation and covariate effects (Figure 2 and 3: colored areas within the black outline) and brain areas with covariate effects only (Figure 2 and 3: colored areas outside the black outline). This was done for effects of VCI and VF on auditory sentence comprehension and phonological processing, resulting in eight ROIs (i.e., 2 types of brain areas x 2 ability measures x 2 contrasts; that is ROI_1: area *with* a significant activation for sentence comprehension and a significant effect of *VCI*, ROI_2: area *without* a significant activation for sentence comprehension but a significant effect of *VCI*, ROI_3: area *with* a significant activation for sentence comprehension and a significant effect of *VF*, ROI_4: area *without* a significant activation for sentence comprehension but a significant effect of *VF*, and the same for

phonological processing for ROI_5 – ROI_8). For each of these ROIs, each participant's individual percentage of BOLD signal change was extracted in response to auditory sentence comprehension and phonological processing, respectively.

In order to compare subjects with relatively higher and lower language ability directly, a median split was performed for each of the two language ability measures. Thus, a higher VCI group (n = 11, 5 male) was compared with a lower VCI group (n = 11, 3 male) and a higher VF group (n = 11, 4 male) was compared with a lower VF group (n = 11, 4 male). For the VCI, three subjects fell exactly onto the median score. Hence, the median split was performed on the raw WASI score (Vocabulary and Similarities subtests combined).

The comparisons of the higher-ability groups with the lower-ability groups revealed the expected pattern. In brain areas where covariate effects overlapped with group activations, the mean BOLD signal change for auditory sentence comprehension and phonological processing was positive in the higher- as well as the lower-ability groups (see Figure 4a and 5a). On the other hand, in brain areas that showed correlations but no group activation, the higher-ability groups showed a positive signal change for both contrasts whereas the lower-ability groups did not (see Figure 4b and 5b).

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Insert Figure 4 and 5 about here

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4. Discussion

The main aim of this study was to investigate the relationship between language ability and brain activity during language processing, using neural responses to sentence processing and phonological processing. Sentence comprehension activated the left anterior temporal lobe in the listening and the reading modality, as expected (e.g., Constable et al., 2004; Humphries, Willard, Buchsbaum, & Hickok, 2001; Vandenberghe, Nobre, & Price, 2002). Phonological processing, on the other hand, activated the left inferior frontal gyrus, pars opercularis, and

precentral gyrus (e.g., Saur et al., 2008). All of these activations are in accordance with current models of language processing and with results from previous neuroimaging studies (Hickok & Poeppel, 2007; Price, 2012; Vigneau et al., 2006).

Building on these findings, it was investigated how individual differences in language ability are related to the recruitment of brain areas and the intensity of brain activity. The results revealed consistent positive correlations of the Verbal Comprehension Index (VCI as measured by the WASI-II) and verbal fluency (VF) with brain activity in the language network. In addition, some brain regions outside the core language network showed negative correlations with VF.

4.1 Positive relationships between language ability and brain activity

Consistent positive correlations were observed between language ability and brain activity during auditory sentence comprehension and during phonological processing in pseudoword repetition. Since the results were very similar for the VCI and VF, they will be discussed together under the term language ability, unless specified otherwise. Higher language ability was associated with increased left anterior temporal lobe activity during auditory sentence comprehension and with increased left frontal lobe activity during phonological processing. Thus, process-specific brain areas were activated to a greater degree by participants with relatively higher language ability than by participants with lower language ability. The increased engagement of brain areas by higher-ability participants was reflected in both, the intensity as well as the extent of neural activations.

Higher *intensity* of neural activity in higher-ability participants was found in brain areas where group activation overlapped with the positive correlation between and language ability and brain activity. These brain areas were activated for the respective language process by the whole sample but more strongly so in individuals with higher language ability, possibly reflecting deeper processing of language stimuli in individuals with higher language ability (Van Ettinger-Veenstra et al., 2016). In contrast, greater *extent* of neural activity in higher-ability participants was found in brain areas with a positive correlation between neural activity

and language ability but no group activation. Further investigations of BOLD response showed that these brain areas were recruited exclusively by individuals with higher language ability. During sentence processing, higher-ability participants showed additional activation in the left inferior temporal gyrus (ITG), which has been shown to be involved in semantic processing (e.g., Whitney, Jefferies, & Kirchner, 2010) and sentence processing (e.g., Ikuta et al., 2006; Halai, Parkes, & Welcourne, 2015). During phonological processing, higher-ability participants showed additional activation in the left precentral gyrus, which is known to support phonological processing (Saur et al., 2008), especially in individuals with higher phonological ability (Szenkovits, Peelle, Norris, & Davis, 2012). The lack of a group activation in the left ITG and the left precentral gyrus during auditory sentence comprehension and phonological processing, respectively, suggests that their involvement might not be crucial for the task. However, the areas' well-established role in the two language processes suggests that their recruitment might allow individuals with higher language ability an enhanced processing of language stimuli.

4.2 Potential modality effects in the relationship between language ability and brain activity

Contrary to our prediction, there were no positive correlations between language ability and brain activity for sentence comprehension in the reading modality. Both, VCI and VF are verbal tasks that rely on receiving auditory input and generating spoken output. In that respect, they are similar to the listening and repetition part of the fMRI paradigm of the current study, but different from the reading part, which was entirely reliant on visual input and visual stimulus processing. The lack of similarity with regards to cognitive demands could explain the lack of a significant positive correlation between language ability and reading activity. Although this explanation remains speculative, it has previously been argued that a similarity in cognitive demands between ability measures and fMRI tasks increases the likelihood of correlations with activity (Neubauer & Fink, 2009). Previous studies that have found significant relationships between language ability and neural activity in reading, have used ability measures and fMRI paradigms with greater overlap in cognitive demands, for example with

respect to modality (Buchweitz et al., 2009) or higher-level, domain-general task demands (Van Ettinger-Veenstra et al., 2016). Future studies could clarify the role that task similarity and processing modality plays for correlations between ability and brain activity.

4.3 Negative relationships between language ability and brain activity

In contrast to the positive correlations reported above, negative correlations were less clear and less consistent across ability measures and language processes. No negative correlations were found between the VCI and neural activity. VF showed negative correlations with neural activity in right auditory areas for auditory sentence comprehension and in right occipital and precentral areas for sentence reading. These effects are in line with previous findings of negative correlations of language ability with right STG activity in a listening task (Zekveld, Rudner, Johnsrude, Heslenfeld, & Rönnberg, 2012) and right visual cortex in a reading task (Prat et al., 2007).

These effects could be interpreted as more efficient or more automated processing in higher-ability individuals (Welcome & Joanisse, 2012). Alternatively, since both negative correlations were located in the right hemisphere, the findings are also in line with the hemispheric spillover hypothesis (Prat, Mason, & Just, 2011; Prat, Mason, & Just, 2012) which predicts stronger involvement of the non-dominant right hemisphere during language processing in individuals with relatively lower language ability. Alternatively, the negative correlations between ability and activity in the right hemisphere could be interpreted as a suppression effect. If a dominance of the left hemisphere in language processing is assumed to be beneficial (e.g., Gutierrez-Sigut, Payne, & MacSweeney, 2015), a reduced involvement, or “deactivation”, of right-hemispheric homologues could be necessary or helpful for language processing. However, since the negative correlations in the current study were not consistent across the two language ability measures and across the different language processes, the interpretation of these results should be seen as tentative.

4.4 Neural efficiency and domain-general versus language-specific task demands

The current study measured neural responses to different language processes in a stimulus-driven manner that was very low in non-linguistic cognitive demands. In contrast, previous studies have usually used language tasks that additionally involved non-linguistic cognitive processes, such as working memory processes (e.g., Prat & Just, 2011; Prat et al., 2012), or decision making (e.g., Buchweitz et al., 2009; Van Ettinger-Veenstra et al., 2016). It is difficult to determine the extent to which these non-linguistic task components contributed to the findings. Thus, differences in brain activity between higher-ability individuals and lower-ability individuals might not solely reflect differences in activity associated with language processing but at least to some extent differences in activity associated with cognitive demand in general.

A review on the relationship between brain activity and cognitive ability suggested a differentiation between cognitive processes and brain regions associated with fluid aspects of intelligence, such as executive functioning in frontal areas, versus processes and regions that are more domain-specific, such as memory functions in parietal areas (Neubauer & Fink, 2009). The authors concluded that neural efficiency might be a concept that primarily applies to frontal brain areas. These areas are often found to show decreases in activity with increasing cognitive ability, whereas process-specific areas have been found to show increases. This pattern was proposed to be particularly true for tasks or cognitive processes that have been automated due to extensive practice. For such processes, subjects increasingly rely on specialized brain regions rather than frontal executive areas and might then show increased activations in these specialized brain regions with increasing ability. While the review discusses memory processes in the parietal lobe as an example, it is conceivable that the same mechanisms apply to other cognitive functions, indicating a general principle of how cognitive ability is reflected in brain activity. The positive relationships between language ability and brain activity found the current study are in line with this principle. In contrast, the fact that the current results showed fewer negative correlations than previous research, might stem from the comparatively low domain-general demands of the fMRI paradigm, which would be expected to show negative relationships with activity.

A recent meta-analysis provided further evidence for increased activity in process-specific brain areas with increased cognitive ability (Neumann, Lotze, & Eickhoff, 2015). Across various areas of expertise (e.g., musical, arithmetic, or chess expertise), individuals with higher levels of ability showed increased activity in brain areas that were associated with their area of expertise (e.g., auditory cortex for auditory stimulation). While all of the twenty-six studies included in the meta-analysis showed positive relationships, only two of these twenty-six studies additionally reported brain areas of decreased activation in higher-ability individuals.

4.5 Differences between language ability measures

The large overlap in positive relationships between ability and activity for the VCI and VF is remarkable, given that language ability is a multidimensional construct and VCI and VF operationalize it in different ways. The two measures were positively correlated, sharing 21% of variance, which can account to some extent for the overlap in results. Furthermore, the relatively basic level of language processing assessed with the task-free fMRI paradigm might be susceptible to a wide range of different language abilities, assessed with different measures.

In contrast, all negative relationships between language ability and brain activity in the current study were observed for VF only, but not for the VCI. All of these negative relationships were located outside the core language network and included areas associated with executive functioning, such as the MFG. Given that the VF test does not only assess language-specific abilities but also executive functions (Aita et al., 2018), the negative relationships between VF and brain activity could reflect those domain-general components of VF. In contrast, the VCI, which does not have such a strong executive functioning component, shows only positive relationships with brain activity. This interpretation would provide further support for a distinction between positive ability-activity relationships for domain-specific abilities and negative relationships for domain-general abilities. However, as noted above, the lack of consistency warrants further investigation and replication.

The current study did not include a separate measure of non-verbal ability. Future studies should combine measures of verbal ability and measures of domain-general, non-verbal cognitive ability in order to allow for a more direct investigation of potentially differential mechanisms for domain-specific and domain-general relationships with brain activity.

4.6 Limitations of the study

When interpreting the present results, the sample composition should be borne in mind. First, all participants were highly educated university students and their VCI was considerably higher than the population average IQ of 100. It is plausible that the mechanisms that underlie the relationship between language ability and neural activity, are the same across the entire range of language ability. Still, the generalizability of the findings to a sample that is more representative of the population should be subjected to further investigation. Second, the variability of language ability in the current sample was smaller than it is in the general population. Performing median splits on the VCI and VF scores allowed us to directly compare those individuals in the sample who had relatively higher ability to those with relatively lower ability. However, for the VCI as well as VF, the means of the higher and the lower groups did not differ as much as would be expected when performing a median split on a more representative sample. The fact that the results still showed consistent differences in neural activations in these comparisons suggests that the relationship between language ability and neural activity is robust even when investigating only a reduced range of the ability spectrum. Finally, the sample size was relatively small, which could make the results more susceptible to false negative as well as false positive findings compared to studies with larger sample sizes (Carp, 2012; Cremers et al., 2017 but Desmond & Glover, 2002; Seghier, Lazeyras, Pegna, Annoni, & Khateb, 2007). However, the concordance of the group activations in the current study with results from relevant reviews and meta-analyses in the field (Hickok & Poeppel, 2007; Price, 2012; Vigneau et al., 2006) does not indicate either false negative or false positive findings in the activations that were the basis for the investigations of activity-ability relationships. Furthermore, the main findings of positive relationships between

language ability and neural activity in process-specific brain areas was consistent across language processes and ability measures, further supporting the reliability of the results. Findings that were less consistent, on the other hand, should be interpreted with caution, as already stated in the discussion above.

4.7 Conclusions

The current study found strong evidence for a positive relationship between language ability and neural activity within the language network across different language processes, modalities, and brain regions. Individuals with relatively higher language ability showed more intense and more extensive activations in left temporal areas during auditory sentence comprehension and in left frontal areas during phonological processing. This increased involvement of process-specific cortical areas suggests deeper processing in individuals with higher language ability compared to individuals with lower language ability. Evidence for decreased activations outside the language network in higher-ability individuals, previously interpreted as neural efficiency, was not as consistent. The results of the current study suggest that previous findings of neural efficiency may have partially been driven by general cognitive demand rather than language processing per se. The paradigm used in the current study allowed for an investigation of the relationship between language ability and brain activity during language processing in the absence of additional task demands. Under these circumstances, higher ability seems to be linked to increased rather than decreased neural activity. Combined with similar findings in a variety of other cognitive domains, the current results suggest that the increased engagement of domain-specific brain regions in individuals with higher ability might be a general mechanism of brain functioning for domain-specific abilities, whereas different principles seem to be true for general cognitive ability.

Declaration of interest

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Tables

Table 1
Example of stimuli used in the sentence condition and in the word condition across participants

	Participant A	Participant B
Sentence condition	The customer tries the spicy soup	The customer tries the spicy meal
	The nephew finds the hidden toy	The nephew finds the hidden box
Word condition	meal … stew …	soup … stew …
	box … sweets …	toy … sweets …

Figures

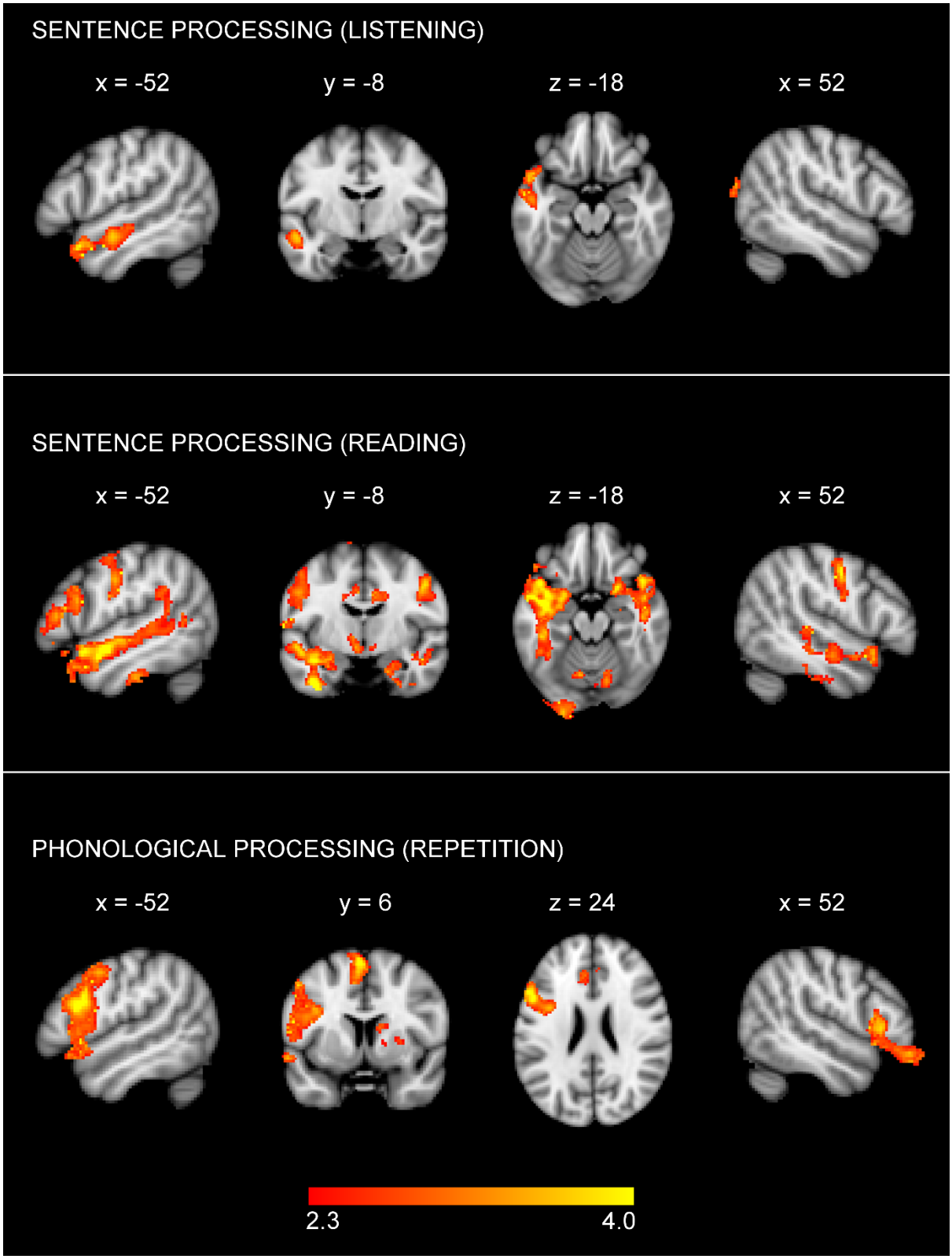

Figure 1. Group activations for the different language processes. All results are cluster-corrected at z = 2.3, p < .05. For coronal and axial slices, the left side of the image is the left side of the brain.

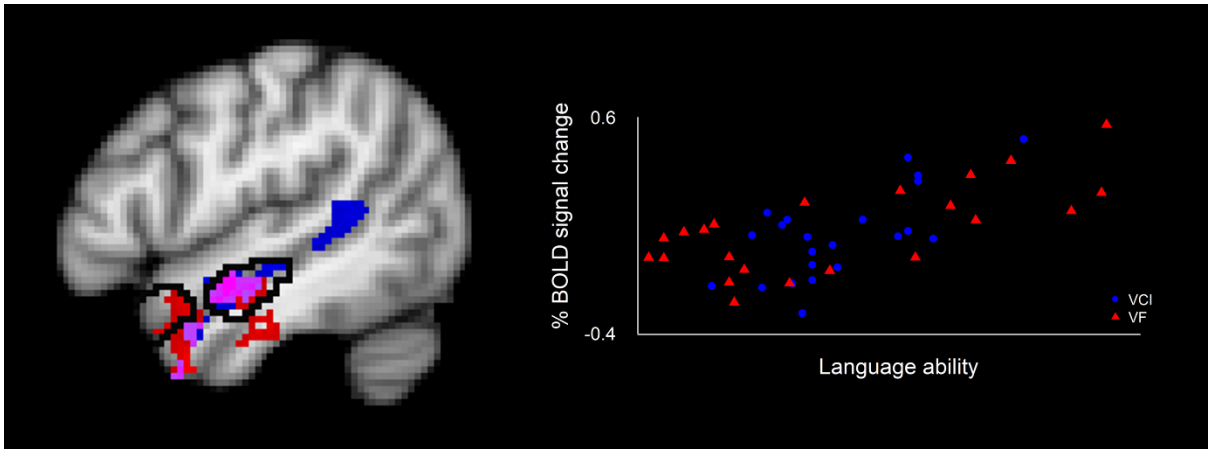

Figure 2. Correlations between language ability and BOLD responses to auditory sentence comprehension (sentence listening > auditory control). Left: significant covariate effects of the VCI are shown in blue (i.e., areas where BOLD signal change for sentence comprehension correlated with the VCI); significant covariate effects of VF are shown in red; areas with significant covariate effects of VCI as well as VF are shown in purple. Some of the areas that showed covariate effects also showed activations for auditory sentence comprehension in the original group analysis. These areas of original group activation are indicated by the black outline (see also Figure 1A). Right: correlations between the VCI (blue) and VF (red) on the one hand and BOLD responses to sentence processing in the respective areas of correlation on the other hand. VCI and VF scores are demeaned for display purposes. For VCI r(20) =.70, p < .001, for VF r(20) = .71, p < .001.

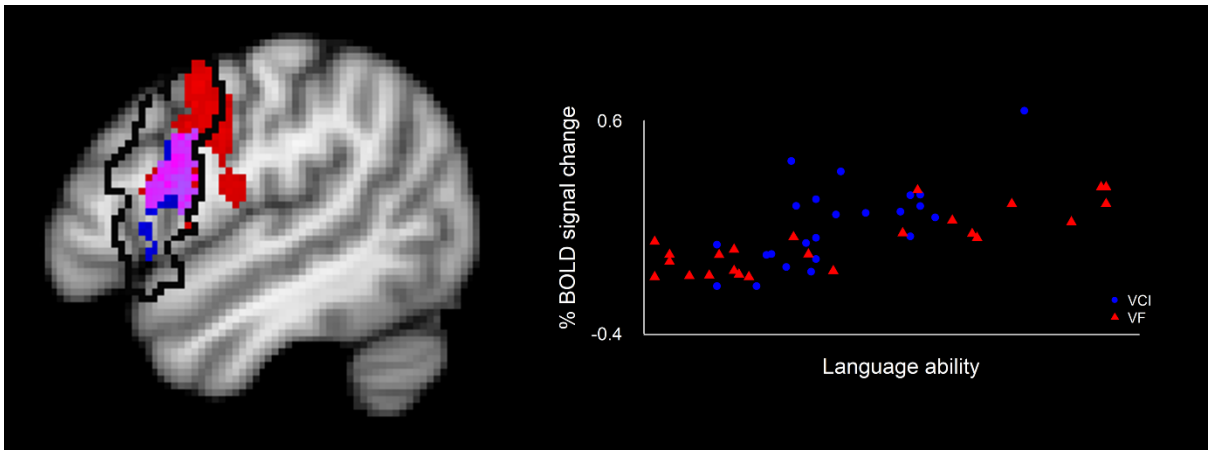

Figure 3. Correlations between language ability and BOLD responses to phonological processing (repeating pseudowords > control). Left: significant covariate effects of the VCI are shown in blue (i.e., areas where BOLD signal change for phonological processing correlated with the VCI); significant covariate effects of VF are shown in red; areas with significant covariate effect of VCI as well as VF are shown in purple. Some of the areas that showed covariate effects also showed activations for phonological processing in the original group analysis. These areas of original group activation are indicated by the black outline (see also Figure 1C). Right: correlations between the VCI (blue) and VF (red) on the one hand and BOLD responses to phonological processing in the respective areas of correlation on the other hand. VCI and VF scores are demeaned for display purposes. For VCI r =.64, p = .001, for VF r = .81, p < .001.

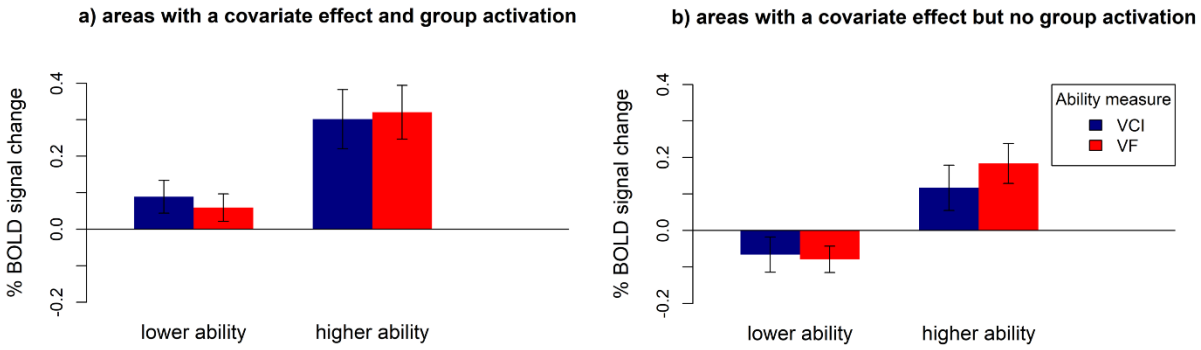

Figure 4. a) Mean BOLD responses (with SEM) to auditory sentence comprehension within areas where covariate effects of VCI and VF respectively overlapped with the group activation for sentence comprehension (i.e. colored areas within the black outline in Figure 2). b) Mean BOLD responses (with SEM) to auditory sentence comprehension within areas with covariate effects of VCI and VF respectively but no significant group activation for sentence comprehension (i.e. colored areas outside the black outline in Figure 2). Results are displayed separately for the two median split groups (i.e. lower and higher ability) per language ability measure.

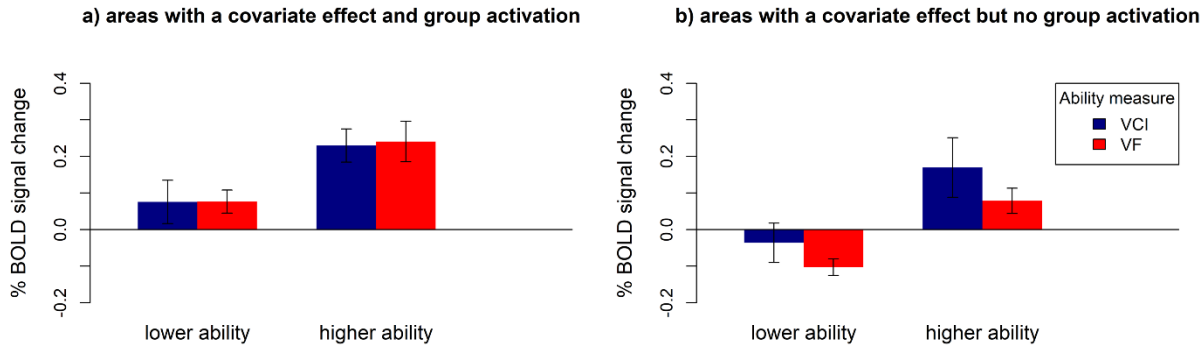

Figure 5. a) Mean BOLD responses (with SEM) to phonological processing within areas where covariate effects of VCI and VF respectively overlapped with the group activation for phonological processing (i.e. colored areas within the black outline in Figure 3). b) Mean BOLD responses (with SEM) to phonological processing within areas with covariate effects of VCI and VF respectively but no significant group activation for phonological processing (i.e. colored areas outside the black outline in Figure 3). Results are displayed separately for the two median split groups (i.e. lower and higher ability) per language ability measure.

Appendix

Table S1
Details of stimulus presentation in listening runs (two runs of 19.2 min, total of 8 blocks per condition).

Condition	Number of stimuli per block	Mean stimulus duration (ms)	Mean ISI duration (ms)
Control stimuli	14	812	2991
Pseudowords	14	811	2999
Words	14	843	2997
Pseudosentences	6	2424	6350
Scrambled sentences	6	3057	6349
Sentences	6	2388	6342

Table S2
Details of stimulus presentation in reading runs (two runs of 15.0 min, total of 8 blocks per condition). (Pseudo-)sentences were divided into three consecutively presented chunks.

Condition	Number of stimuli per block	Mean stimulus duration (ms)	Mean ISI duration (ms)
Control stimuli	14	1000	2487
Pseudowords	14	1000	2506
Words	14	1000	2517
Pseudosentences	6	3 x 14000	5865
Sentences	6	3 x 14000	5877

Table S3
Details of stimulus presentation in repetition runs (two runs of 13.1 min, total of 8 blocks per condition)

Condition	Number of stimuli per block	Mean stimulus duration (ms)	Mean ISI duration (ms)
Control stimuli	7	840	5563
Pseudowords	7	811	5590
Words	7	843	5478
Sentences	3	2388	12188

Table S4
Details for group activations for sentence processing (listening)

	Size (k)	Sig. (p)	Peak (x y z)	Z-value	Brain areas covered
Cluster 1	586	.026	-52 6 -22	5.01	LH: temp pole, aSTG, aMTG, pSTG, pMTG
Cluster 2	1415	<.001	18 -40 50	3.89	RH: Precuneu, SPL, postcentral g, cing g
Cluster 3	600	.023	46 -88 20	3.83	RH: lat occip c, occip pole

Peak locations are given in mm in MNI-152 standard space. Probabilistic locations are derived from the Harvard-Oxford Cortical Structural Atlas. Abbreviations: LH/RH=left/right hemisphere, a=anterior, p=posterior, c=cortex, g=gyrus, lat = lateral, IFG=inferior frontal gyrus, tri=triangularis, op=opercularis, SFG = superior frontal gyrus, MFG=middle frontal gyrus, cing=cingulate, SMG=supramarginal gyrus, STG = superior temporal gyrus, MTG = middle temporal gyrus, ITG, inferior temporal gyrus, SPL = superior parietal lobule, temp = temporal, occip = occipital.

Table S5
Details for group activations for sentence processing (reading)

	Size (k)	Sig. (p)	Peak (x y z)	Z-value	Brain areas covered
Cluster 1	21381	<.001	-10 -92 0	6.46	Bilateral: occip pole, cuneal c, calcarine c, lingual g, occip fusisorm g, LH: p parahipp g, insular c, frontal orbital c, temp pole, planum polare/temp, aSTG, pSTG, pMTG, pITG, temp fusiform c, temporo-occip MTG/ITG, SMG, parietal operculum, angular g
Cluster 2	728	.016	38 -12 38	5.06	RH: postcentral g, precentral g, central opercular c
Cluster 3	5290	<.001	8 -44 62	4.93	Bilateral: precuneous c, post-central g, SPL, precentral g, p cing g
Cluster 4	2281	<.001	56 -30 0	4.53	RH: pSTG, pMTG, pITG, aSTG, planum polare, insular c, parahipp g, temp pole, frontal orbital c
Cluster 5	679	.024	-52 -14 40	4.14	LH: postcentral g, precentral g

Peak locations are given in mm in MNI-152 standard space. Probabilistic locations are derived from the Harvard-Oxford Cortical Structural Atlas. Abbreviations: see Table S4.

Table S6

Details for group activations for phonological processing (repetition)

	Size (k)	Sig. (p)	Peak (x y z)	Z-value	Brain areas covered
Cluster 1	2995	<.001	-48 12 14	4.95	LH: IFG op, IFG tri, frontal operculum, temp pole, precentral g, MFG
Cluster 2	2269	<.001	-4 22 50	4.81	Bilateral: SFG, juxtapositional lobule c, paracing g, cing c

Cluster 3	2124	<.001	36	22	-2	4.51	RH: Insular c, frontal orbital c, IFG tri, IFG op, frontal operculum, frontal pole

Peak locations are given in mm in MNI-152 standard space. Probabilistic locations are derived from the Harvard-Oxford Cortical Structural Atlas. Abbreviations: see Table S4.

Table S7
Details for correlations between brain activity for auditory sentence processing and language ability measures

	Size (k)	Sig. (p)	Peak (x y z)	Z-value	Brain areas covered
VCI (WASI-II)					
Positive	1150	<.001	-50 -4 -12	4.78	temporal pole, aSTG, aMTG, aITG, pSTG, pMTG, pITG, SMG
Negative	-	-	-	-	-
Verbal Fluency					
Positive	1211	<.001	-42 -16 -30	4.52	temporal pole, aSTG, aMTG, aITG, pSTG, pMTG, pITG, SMG
Negative	888	<.001	70 -28 6	4.52	SMG, pSTG, planum temporale, Heschl's g, central opercular c, precentral g, IFGop

Peak locations are given in mm in MNI-152 standard space. Probabilistic locations are derived from the Harvard-Oxford Cortical Structural Atlas. Abbreviations: see Table S4.

Table S8
Details for correlations between brain activity for visual sentence processing and language ability measures

	Size (k)	Sig. (p)	Peak (x y z)	Z-value	Brain areas covered
VCI (WASI-II)					
Positive	-	-	-	-	-
Negative	-	-	-	-	-

Verbal Fluency					
Positive	-	-	-	-	-
Negative	3022	<.001	12 -82 2	5.21	lingual g, intracalcarine c, parahipp g
	703	.004	36 -62 42	4.67	lat occip c
	506	.026	40 4 36	4.29	Precentral g, MFG

Peak locations are given in mm in MNI-152 standard space. Probabilistic locations are derived from the Harvard-Oxford Cortical Structural Atlas. Abbreviations: see Table S4.

Table S9
Details for correlations between brain activity for phonological processing (repetition) and language ability measures

	Size (k)	Sig. (p)	Peak (x y z)	Z-value	Brain areas covered
VCI (WASI-II)					
Positive	652	.004	-50 4 28	4.95	IFGop, precentral g, insular c
Negative	-	-	-	-	-
Verbal Fluency					
Positive	1608	<.001	-50 2 20	4.96	IFGoper, precentral g, postcentral g, central opercular c, SMG
	1241	<.001	4 -90 -4	3.48	Lingual g, intraccalcarine c, occip pole
Negative	-	-	-	-	-

Peak locations are given in mm in MNI-152 standard space. Probabilistic locations are derived from the Harvard-Oxford Cortical Structural Atlas. Abbreviations: see Table S4.